A 19-Year Study of the Dynamics of an Invasive Alien Tree, *Bischofia javanica*, on a Subtropical Oceanic Island[1]

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Abstract: A 19-yr study of the dynamics of an invasive alien species, *Bischofia javanica* Blume, in a secondary forest was conducted in the Bonin Islands, Japan. The study was begun in 1984 when another alien species, *Pinus luchuensis* Mayer, had begun to die because of infection by a pine nematode as well as typhoon damage in 1983. Diameters at breast height (DBHs) of all trees in a 20 by 20 m plot and heights of all saplings (<1.3 m, ≥0.3 m in height) were measured almost every 3 yr. The total basal area of *P. luchuensis* decreased over time, and all trees had fallen over by 1998. The total basal area of *B. javanica* increased more than 10-fold over 19 yr without changes in tree or sapling density. Up to 1990, growth rates of trees of *B. javanica* were higher than those of two native canopy trees (*Pouteria obovata* and *Machilus kobu*), but a third native canopy tree (*Schima mertensiana*) had growth rates comparable with those of *B. javanica*. After 1990, there were few differences between growth rates of *B. javanica* and native species. However, mortality and recruitment of *B. javanica* were lower than those of native species of canopy trees during the survey period. The higher growth rate, lower mortality, and lower recruitment led to a shift from a skewed size distribution of the individuals of *B. javanica* toward a more bell-shaped size distribution. Our results suggest that regeneration and maintenance of *B. javanica* populations in the secondary forests depend on canopy gaps occasionally created by disturbances.

Oceanic islands are extremely vulnerable to invasions of human-introduced animals and plants. They often have received public attention as their endemic species are crowded out by the introduced species (Loope et al. 1988, Vitousek 1990). Recently, invasion by introduced alien species has become a priority concern for conservation biologists in many oceanic islands, such as the Hawaiian Islands (e.g., Huenneke 1990, Almasi 2000) and the Galápagos Islands (e.g., Itow 1995, Shimizu 1997).

Biological invasion by an alien species often facilitates invasion by other alien species (Mack and D'Antonio 1998, Parker et al. 1999, Simberloff and Von Holle 1999, Richardson et al. 2000) by changing a community or an ecosystem (Vitousek 1990, Vitousek et al. 1997, Levine et al. 2003). The facilitation of invasion may be caused by an increase in the amount of available resources (Davis et al. 2000). For example, damage to an established canopy structure by herbivory of an alien animal species or fire caused by flammable grasses increases the amount of available light for the understory vegetation, which often facilitates further invasions by other alien plants (e.g., Cross 1981, Hughes et al. 1991).

In an environment with abundant resources, alien plants often perform better

[1] This study was supported by a research project on Conservation Methods of Subtropical Island Ecosystems, headed by Seiichi Nohara, National Institute for Environmental Studies, Japan Environmental Agency. Manuscript accepted 12 December 2005.

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Pacific Science (2006), vol. 60, no. 4:455–470

than native plants (e.g., Caldwell et al. 1981, Williams and Black 1994, Pattison et al. 1998, Baruch and Goldstein 1999, Durand and Goldstein 2001). For example, the growth rates of seedlings of alien species are higher than those of natives in nutrient-rich soil (Fogarty and Facelli 1999, Milberg et al. 1999, Lowe et al. 2003), and the mortality rates of alien species can be lower (Goergen and Daehler 2002). The higher growth rates and/or lower mortality rates of the alien species enhance their establishment and dominance (e.g., Aplet et al. 1998, Gentle and Duggin 1998, Kolb et al. 2002).

In forests, canopy gaps increase the available light on the forest floor. Subsequent canopy closure by growth of the established plants reduces the amount of available light. Alien species that perform better than native species in environments with abundant resources (e.g., canopy gaps) may not be able to perform better than native species under a closed canopy. Indeed, relatively few alien plants seem to have the capacity to invade undisturbed native communities (Rejmánek 1989) due to high mortality (Mazia et al. 2001, Green et al. 2004) or low recruitment (Mazia et al. 2001, Bustamante and Simonetti 2005) and low growth rates (Green et al. 2004) in undisturbed native communities. Changes in the amount of available light on a forest floor by the opening and closing of canopy have substantial effects on the population dynamics of those alien species that perform better than native species under the canopy gap but do not perform well under the closed canopy. To quantify the effects of gap opening and closure on invasion, particularly for tree or long-lived species, it is necessary to analyze the long-term population dynamics of an alien species by repeated censuses.

An alien tree species, *Bischofia javanica* Blume (Euphorbiaceae), aggressively invades mesic sites in primary and secondary forests in the Bonin Islands, a subtropical oceanic archipelago in the Pacific, located about 1,000 km south of Tokyo and belonging to Japan (Shimizu 1988, Tanimoto and Toyoda 1996, Mueller-Dombois and Fosberg 1998). In particular, *Bischofia* seedlings frequently established and grew rapidly in forest gaps created by nematode-induced dieback of another alien tree, *Pinus luchuensis* Mayer (Pinaceae), which had previously been the dominant species in secondary forests. Therefore, we predicted that: (1) under a canopy gap created by the death of *P. luchuensis*, *B. javanica* would exhibit lower mortality as well as higher recruitment and growth rates than native species, and (2) under a subsequent closure of the canopy gap, *B. javanica* would exhibit higher mortality and lower recruitment and growth rates than native species, which would affect the community structure of the stand.

To test these predictions, we compared the population dynamics of *B. javanica* with that of native species in a secondary forest where many *P. luchuensis* died over a period of 19 yr.

MATERIALS AND METHODS

Plant Species

The alien tree species *Bischofia javanica* is a dioecious evergreen native to southern China, Taiwan, Southeast Asia, Fiji, Tonga, Samoa, and tropical Australia. The height of this species can be 15–20 m, with a trunk diameter of 1 m under favorable conditions. This species was introduced to the Bonin Islands in the early 1900s (Kimura 1986, Shimizu 1988) and by 1945 had been planted in at least 10 locations on Chichijima Island, the largest island in the archipelago (Toyoshima 1938, Mueller-Dombois and Fosberg 1998:234–240). Thereafter, plants of this species spread into the surrounding mesic primary and secondary forests. Although this species is not a dominant component in a climax forest in its native region, it often appears even in climax forests in the Bonin Islands (Shimizu 1988, Tanimoto and Toyoda 1996).

Most of the mesic secondary forests on Chichijima Island became established after 1945 in abandoned fields, and they were dominated by the introduced species *P. luchuensis* and a native species, *Schima mertensiana* (Sieb. & Zucc.) Koidz. (Theaceae) (Shimizu 1983). These forests are categorized as *Pinus-Schima* forest (Shimizu and Tabata 1991). In

1979 a pine wood nematode, *Bursaphelenchus xylophilus*, was accidentally introduced to Chichijima Island, and almost all of the *P. luchuensis* trees were killed by 1984 (see photo 5. A5 in Mueller-Dombois and Fosberg 1998). In addition, a large typhoon in 1983 damaged the canopy of the secondary forests, which resulted in increases in amount of available light for the forest understory (Shimizu 1986). Relative light intensity on the forest floor of the *Pinus-Schima* forests where the pine nematode had killed the *P. luchuensis* rose by more than 50% after the typhoon in 1983 (Shimizu 2005). After the death of the *P. luchuensis*, most of the stands of the *Pinus-Schima* forests were composed mostly of *S. mertensiana* (Shimizu 1986), and *B. javanica* aggressively invaded some of these forests (Kimura 1986).

Plot Establishment

A permanent 20 by 20 m plot was established for long-term monitoring in 1984 in a forest in the Fukiagedani Valley (27° 04′ N, 142° 12′ E, 120 m above sea level). Many *B. javanica* trees able to produce seeds were found around the plot, and dispersal and germination of seeds were often observed even in the plot. The plot also included some species that were principal components of secondary forests: *Schima mertensiana*, *Pouteria obovata*, *Rhaphiolepis wrightiana*, *Machilus kobu*, *Ardisia sieboldii*, *Osmanthus insularis*, and *Ligustrum micranthum* (Appendix 1). Most of the *P. luchuensis* trees had died but were standing in the plot in 1984. Some trees of *B. javanica* and other native species within or around the plot produced seeds. In this study, woody plants were categorized by their heights into three groups: trees ($\geq$1.3 m), saplings ($<$1.3 m, $\geq$0.3 m), and seedlings ($<$0.3 m). All trees and saplings in the plot were tagged. The heights of all saplings and diameters at breast height (DBHs) of all trees were measured. The DBHs of the dead *P. luchuensis* trees were also measured to estimate their biomass when they were alive. Size remeasurements of the trees and saplings were carried out in winter or spring in 1987, 1990, 1995, 1998, 2000, and 2003. Seedlings in the plot were tagged and counted in winter 1998, 2000, and 2003.

Relative photosynthetic photon flux densities under a closed canopy and under a gap were estimated from hemispherical photographs (Anderson 1964, Anderson and Miller 1974, Chazdon and Field 1987). The photographs were taken under a closed canopy within the plot at six points around noon on cloudy days in February 2000 using a camera (Nikon FE, Nikon, Tokyo, Japan) and 180° angle lens (Fisheye-NIKKOR f8, Nikon, Tokyo, Japan). We did not investigate light environments in 1984. Instead, we took photographs under a gap near the plot created by the death of a *P. luchuensis* and assumed the light environment to be the same as that in 1984 under a canopy gap where a *P. luchuensis* had died. HemiView 2.1 Canopy Analysis Software (Delta-T Devices, Burwell, Cambridge, United Kingdom) was used to calculate the relative diffuse radiation at 0.5 m above ground level from the photographs.

Additional Vegetation Surveys

To more broadly describe species composition of the *Pinus-Schima* forests after death of *P. luchuensis*, we established 35 plots (100–400 m^2; total area of the 35 plots was 0.4987 ha) in the secondary forests on Chichijima Island and measured diameters at 1.3 m above ground level (DBH) of all trees in 2000 and 2003.

Data Analysis

We compared *B. javanica* with principal native canopy tree species having niches that are likely to overlap with those of *B. javanica* in secondary forests. We defined three native species, *S. mertensiana*, *P. obovata*, and *M. kobu*, as native canopy tree species because they included individuals larger than 25 cm DBH in the 35 *Pinus-Schima* forest plots (Appendix 3). In addition, the number of trees of these species in the 20 by 20 m permanent plot was large enough for statistical analyses. The three species were also categorized as canopy trees of the secondary forests by Shimizu and Tabata (1991). Although individuals

of *Livistona chinensis* were larger than 25 cm DBH, they were less likely to grow in diameter at breast height because they were monocots. Changes in basal area at 1.3 m above ground level, density, and size structure were compared between *B. javanica* and the three native canopy species for 19 yr. Mortality, recruitment, and growth rates were also compared between *B. javanica* and the three native species during each survey period. Mortality of trees between each survey period was calculated as the number of trees dying during a survey period divided by the number of trees at the beginning of a survey period. Recruitment of trees between each survey period was calculated as the number of trees recruited (i.e., exceeding 1.3 m height) during a survey period divided by the number of trees at the end of a survey period. Differences in mortality and recruitment of trees during each survey period between *B. javanica* and each of the three native species were analyzed by Fisher's exact probability test. Annual absolute growth rates in DBH (cm $year^{-1}$) in each survey period were analyzed by one-way analysis of variance (ANOVA), and Holm's multiple test (Dalgaard 2002) was also conducted in all possible combinations of treatments. To evaluate changes in size structure of *B. javanica* and the three native canopy species for 19 yr, size distributions of DBH of *B. javanica* and the three native canopy species in 1984 were compared with those in 2003 by two-sample Kolmogorov-Smirnov test. All statistical analyses were carried out with the software R 2.0.1 (http://www.r-project.org/).

RESULTS

Changes in Basal Area and Relative Dominance

In 1984 the basal area of the dead *P. luchuensis* trees was 34.9 cm^2 m^{-2} and that of all live trees was 30.2 cm^2 m^{-2}. The basal area of all live trees had increased by 2003 (Figure 1*a*). However, the basal area of live *P. luchuensis* trees decreased because of death, and all *P. luchuensis* had fallen over by 1998 (Figure

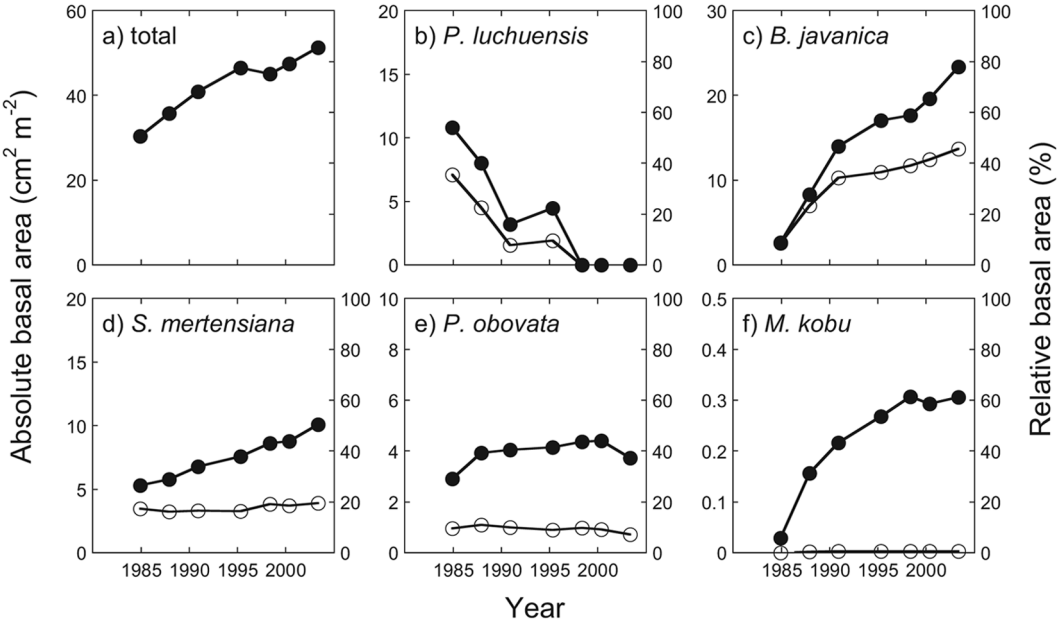

FIGURE 1. Changes in basal area of trees (>1.3 m height) in the permanent plot during 19 yr: *a*, total; *b*, *P. luchuensis*; *c*, *B. javanica*; *d*, *S. mertensiana*; *e*, *P. obovata*; *f*, *M. kobu*. Closed circles indicate absolute values and open circles indicate relative values of the total basal area.

1*b*). The basal area of trees of *B. javanica* in 2003 was almost nine times larger than that in 1984 (Figure 1*c*). The relative dominance of *B. javanica* increased from 8.6% to 45.5% between 1984 and 2003. The basal area of other alien species other than *B. javanica* and *P. luchuensis* was low and changed very little during the 19 yr (Appendix 1).

More than 75% of the basal area consisted of native tree species *Schima mertensiana*, *Pouteria obovata*, and *Rhaphiolepis wrightiana* (Appendix 1). Basal area of *S. mertensiana* in 2003 was 1.9 times as large as that in 1984, but its relative dominance did not change in the 19 yr (Figure 1*d*). Small changes in the basal area of *P. obovata* were observed over the 19 yr (Figure 1*e*). The basal area of *Machilus kobu* was low, but it increased constantly over 19 yr (Figure 1*f*).

Changes in Densities of Trees, Saplings, and Seedlings

The total number of trees markedly increased from 1984 to 1990 and decreased slightly after 1990 (Figure 2*a*). The number of *P. luchuensis* trees gradually decreased, and all had disappeared by 1998 (Figure 2*b*). There were only small changes in the number of *B. javanica* trees, and *B. javanica* represented ca. 40% of all trees in the plot over the 19 yr (Figure 2*c*). The number of trees of *S. mertensiana* increased, and the relative dominance increased from 3.2% to 6.5% between 1984 and 2003 (Figure 2*d*). The numbers of trees of *P. obovata* and *M. kobu* increased from 1984 to 1990 but decreased after 1990 (Figure 2*e*, *f*). The relative densities of trees of the two native species did not change between 1984 and 2003.

The total number of saplings of all species decreased from 1984 to 1995, increased from 1995 to 2000, and decreased again toward 2003 (Figure 3*a*). More than 70% of the total number of saplings consisted of three dominant native species, *R. wrightiana*, *Ligustrum micranthum*, and *P. obovata*, over the 19 yr (Appendix 2). The percentage of saplings of *B. javanica* was not larger than 10% of the total number of saplings, decreased rapidly

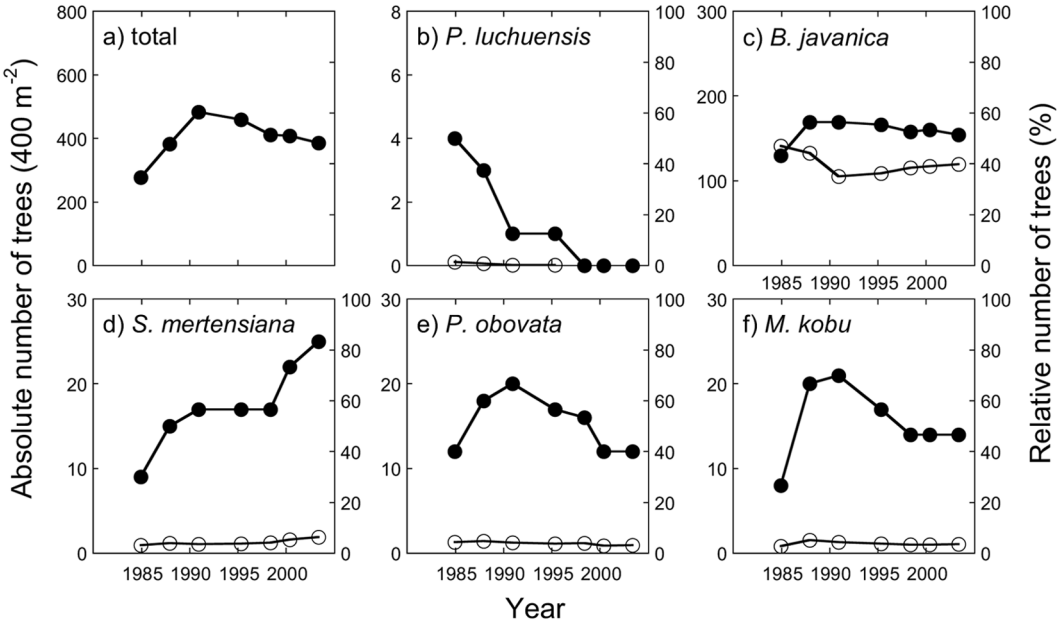

FIGURE 2. Changes in the number of trees in the permanent plot during 19 yr: *a*, total; *b*, *P. luchuensis*; *c*, *B. javanica*; *d*, *S. mertensiana*; *e*, *P. obovata*; *f*, *M. kobu*. Closed circles indicate absolute values and open circles indicate relative values.

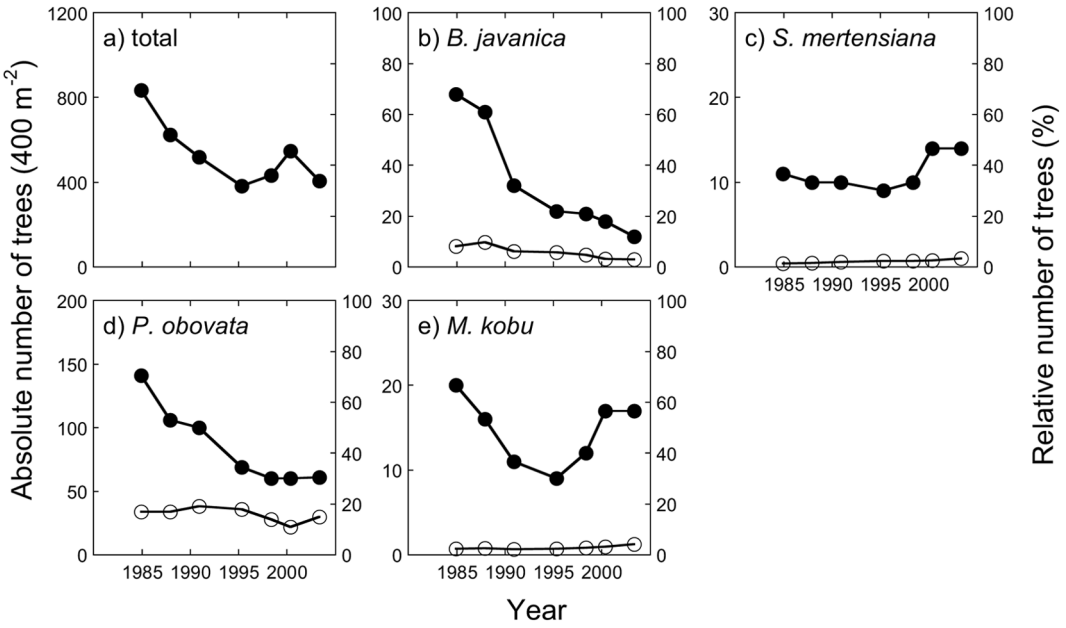

FIGURE 3. Changes in the number of saplings in the permanent plot during 19 yr: *a*, total; *b*, *B. javanica*; *c*, *S. mertensiana*; *d*, *P. obovata*; *e*, *M. kobu*. Closed circles indicate absolute values and open circles indicate relative values.

between 1984 and 1987, and then decreased steadily through 2003 (Figure 3*b*). Number of saplings of *S. mertensiana* was 1.3% of the total numbers of saplings and did not change during 19 yr (Figure 3*c*). The number of saplings of *P. obovata* decreased over 19 yr (Figure 3*d*). The number of saplings of *M. kobu* decreased between 1984 and 1995 and then increased after 1995 (Figure 3*e*). No saplings of *P. luchuensis* were observed in the permanent plot during the 19 yr.

In the permanent plot, seven seedlings of *B. javanica* were counted in 1998, 146 in 2000, and 12 in 2003. Most seedlings of native species belonged to *R. wrightiana*, *L. micranthum*, or *P. obovata*. In 1998, 63 seedlings of *P. obovata* were noted, 63 in 2000, and 52 in 2003. There were few seedlings of *S. mertensiana* and *M. kobu*.

Changes in Size Structure

There were only four living *P. luchuensis* trees in 1984, and their DBHs were all larger than 16 cm. They had died by 1998, and no recruitment of *P. luchuensis* occurred after 1984 in the permanent plot. All of the *B. javanica* trees were smaller than 8 cm DBH in 1984 except for one individual (DBH = 17.7 cm), and the size distribution was weakly skewed (Figure 4*a*). Between 1984 and 2003, the size distribution of *B. javanica* became increasingly bell-shaped, and it changed significantly (two-sample Kolmogorov-Smirnov test, $D = 0.63$, $P < 0.001$). Size distributions of *S. mertensiana* and *P. obovata* were various but more evenly distributed throughout the sizes (Figure 4*b*, *c*). No significant change in the size distributions of *S. mertensiana* and *P. obovata* was observed between 1984 and 2003 (two-sample Kolmogorov-Smirnov test, $D = 0.30$, $P = 0.41$ and $D = 0.42$, $P = 0.26$, respectively). Diameters at breast height of all *M. kobu* trees were smaller than 4 cm in 1984, and the size distribution of the species was L-shaped in 1984 and throughout the 19-yr study period (two-sample Kolmogorov-Smirnov test, $D = 0.59$, $P = 0.059$) (Figure 4*d*).

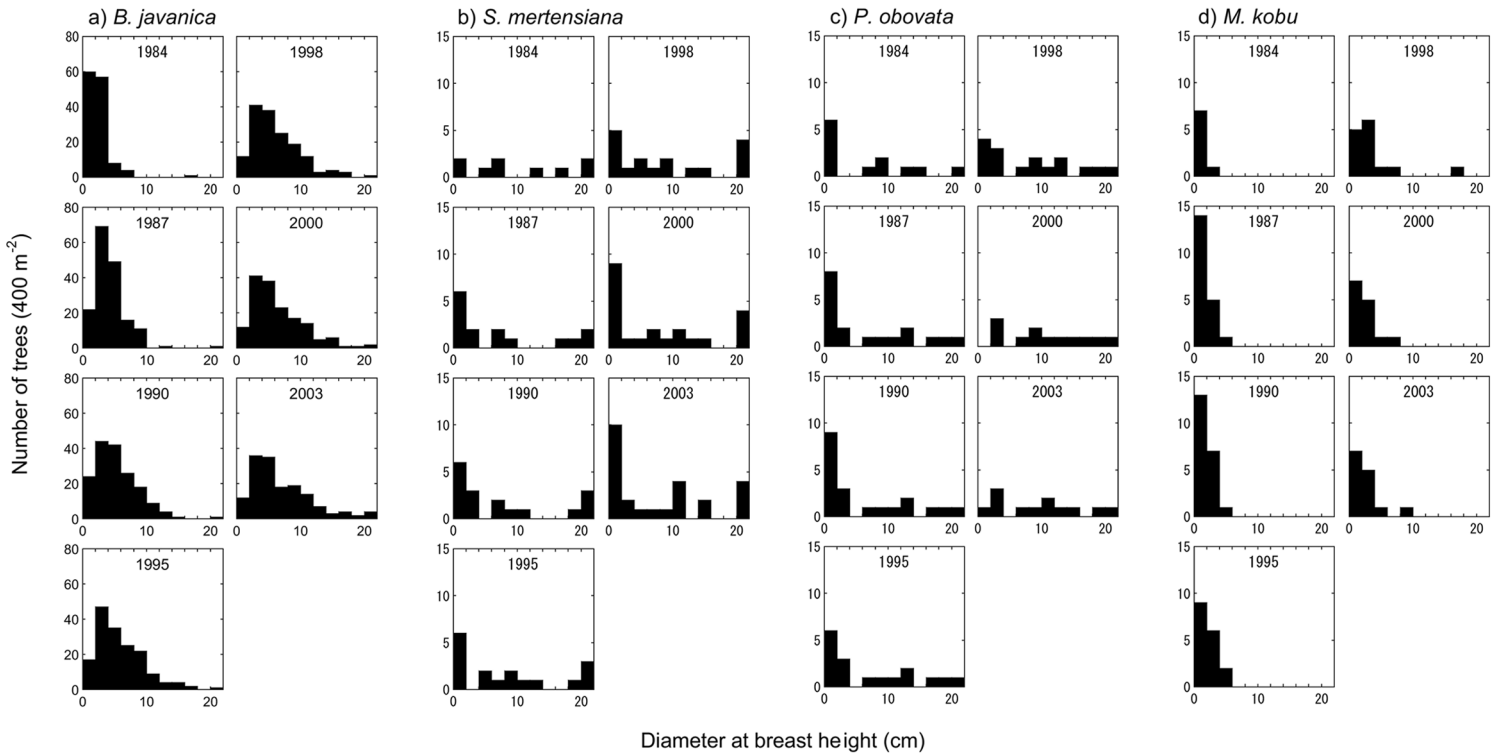

FIGURE 4. Frequency distributions of size of trees in the permanent plot for each of seven survey times: *a*, *B. javanica*; *b*, *S. mertensiana*; *c*, *P. obovata*; *d*, *M. kobu*.

TABLE 1

Mortality of Trees of *B. javanica* and Three Native Canopy Species in Two DBH Size Classes between Survey Periods

DBH Size	Survey Period	*B. javanica*	*S. mertensiana*		*P. obovata*		*M. kobu*	
<8 cm	1984–1990	0.054	0	n.s.	0	n.s.	0.125	n.s.
	1990–1995	0.037	0.091	n.s.	0.385	***	0.190	*
	1995–2000	0.113	0	n.s.	0.600	***	0.353	*
	2000–2003	0.061	0.077	n.s.	0	n.s.	0.071	n.s.
>8 cm	1984–1990	0	0	n.s.	0	n.s.		
	1990–1995	0	0	n.s.	0	n.s.		
	1995–2000	0.024	0	n.s.	0	n.s.		
	2000–2003	0	0	n.s.	0.125	n.s.		

*, $P < 0.05$; ***, $P < 0.001$; n.s., not significant between *B. javanica* and each of the three native canopy species by Fisher's exact probability test.

TABLE 2

Recruitment of Trees of *B. javanica* and Three Native Canopy Species between Survey Periods

Survey Period	*B. javanica*	*S. mertensiana*		*P. obovata*		*M. kobu*	
1984–1990	0.272	0.471	n.s.	0.400	n.s.	0.667	***
1990–1995	0.012	0.059	n.s.	0.118	*	0	n.s.
1995–2000	0.056	0.227	*	0.083	n.s.	0.214	n.s.
2000–2003	0.006	0.160	**	0.083	n.s.	0.071	n.s.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant between *B. javanica* and each of the three native canopy species by Fisher's exact probability test.

Mortality, Recruitment, and Growth

Mortality of *B. javanica* trees smaller than 8 cm DBH was not different from that of *S. mertensiana* smaller than 8 cm DBH during the 19 yr and significantly lower than that of *P. obovata* and *M. kobu* between 1990 and 2000 (Table 1). Mortality of *B. javanica*, *S. mertensiana*, and *P. obovata* larger than 8 cm DBH was very low, and there were no significant differences between *B. javanica* and the two native species during the 19 yr.

Almost no recruitment of *B. javanica* occurred except for the period between 1984 and 1990. Recruitment rate of *B. javanica* was significantly lower than that of *S. mertensiana* after 1995 (Table 2). The recruitment rate of *B. javanica* was also significantly lower than that of *P. obovata* between 1990 and 1995 and that of *M. kobu* between 1984 and 1990.

Absolute growth rates of *B. javanica* trees smaller than 8 cm DBH were 0.55 cm yr^{-1} between 1984 and 1990 but decreased after 1990 (Table 3). There were no significant differences in absolute growth rates between *B. javanica* and *S. mertensiana* until 1990. Absolute growth rates of *P. obovata* and *M. kobu* were lower than those of *B. javanica* until 1990, although there were no significant differences between growth rates of *B. javanica* and *M. kobu*. After 1990, absolute growth rates of *B. javanica* and the two native species were similar. No significant difference in absolute growth rates of trees larger than 8 cm DBH were observed between *B. javanica* and native species except between 1995 and 2000.

Light Conditions

In February 2000, the mean of the relative diffuse radiation at 0.5 m above ground level under a closed canopy was estimated as 1.72%, and that in a canopy gap as 23.69%. The mean of the relative diffuse radiation in

TABLE 3

Mean (±SE) of Absolute Growth Rate (cm/yr) of Trees of *B. javanica* and Two Native Canopy Species in Two DBH Size Classes between Survey Periods

DBH Size	Survey Period	*B. javanica*	*S. mertensiana*	*P. obovata*	*M. kobu*
<8 cm	1984–1990	0.55 ± 0.03a	0.46 ± 0.13a	0.006 ± 0.04b	0.28 ± 0.07a
	1990–1995	0.09 ± 0.02a	0.55 ± 0.03a	0.02 ± 0.01a	0.05 ± 0.04a
	1995–2000	0.05 ± 0.01a	0.20 ± 0.07b	0.01 ± 0.02ab	0.06 ± 0.03ab
	2000–2003	0.05 ± 0.03a	0.06 ± 0.05a	−0.06 ± 0.05a	0.03 ± 0.04a
>8 cm	1984–1990‡	2.13	0.43 ± 0.05	0.07 ± 0.10	
	1990–1995	0.25 ± 0.05a	0.29 ± 0.03a	0.03 ± 0.03a	
	1995–2000	0.18 ± 0.03a	0.35 ± 0.07b	0.04 ± 0.04a	
	2000–2003	0.39 ± 0.05a	0.42 ± 0.09a	0.04 ± 0.02a	

Values followed by different letters indicate significantly different ($P < 0.05$) treatment means based on Holm's multiple test following ANOVA.

‡ Sample size too small for statistical test.

the canopy gap near the study plot was 14 times higher than that under the closed canopy.

Additional Vegetation Surveys

Surveys of the former *Pinus-Schima* forests across broader areas in 2000 and 2003 showed that the forest consisted of native tree species *S. mertensiana*, *Pouteria obovata*, *Machilus kobu*, *Elaeocarpus photiniifolius*, and *Livistona chinensis*. Native species of shrubs such as *Rhaphiolepis wrightiana*, *Ligustrum micranthum*, *Ardisia sieboldii*, and *Osmanthus insularis* were also included. In some of the 35 plots, *Bischofia javanica* dominated the canopy layer, and an alien species, *Psidium cattleianum*, occurred in the shrub layer. There were no differences in species composition between the 20 by 20 m permanent plot and the 35 additional survey plots (Appendix 3). It is, therefore, likely that the changes documented in the 20 by 20 m permanent plot are representative of the *Pinus-Schima* forests that were aggressively invaded by *B. javanica* after death of *P. luchuensis*.

DISCUSSION

Death of *P. luchuensis* after infection by a pine nematode combined with damage from a large typhoon in 1983 produced many canopy gaps in *Pinus-Schima* forests. High relative diffuse radiation measured in a canopy gap created by death of *P. luchuensis* in 2000 implies that the death of *P. luchuensis* probably also caused marked increases in radiation on the forest floor in the study plot.

For several years after the typhoon in 1983, the relative light intensity on the forest floor of *Pinus-Schima* forests decreased due to growth of sedges, ferns, and large saplings of tree species, and the light conditions on the forest floor became more or less the same as before the death of *P. luchuensis* (Shimizu 2005). Because there were no dead trees larger than 20 cm DBH in the plot except for *P. luchuensis* during the study period (data not presented), it is unlikely that the death of trees other than *P. luchuensis* contributed significantly to increases in light availability. Low relative diffuse radiation under a closed canopy in the plot in 2000 implies that from 1984 to 2003 the decrease in light by closure of canopy was associated with an increase in the basal areas by regrowth of all alien and native woody species except *P. luchuensis*.

In pot-culture experiments that suddenly increased light availability from shade to full sun, seedlings of *B. javanica* and *S. mertensiana* exhibited rapid photosynthetic acclimation in shade leaves by minimizing photoinhibition while also rapidly developing new sun leaves with high photosynthetic capacity, in comparison with other pioneer and late-successional species in the Bonin Islands

(Yamashita et al. 2000). This may have enabled higher growth rates of *B. javanica* trees in the smaller size classes than native canopy tree species except for *S. mertensiana* until 1990, when the forest gaps caused by the death of *P. luchuensis* trees had substantially closed. On the other hand, growth rates of larger trees of *B. javanica* did not differ from rates of native canopy tree species, which indicates that there were little differences in growth between *B. javanica* and native canopy tree species once they reached the forest canopy.

The numbers of saplings and small trees of *B. javanica* decreased because of no recruitment from *B. javanica* seedlings during this time. In and around the study plot, there were several *B. javanica* trees producing seeds (K.H., pers. obs.). Therefore, seed dispersal and germination of seeds could potentially occur in the plot, and germination of *B. javanica* was, indeed, often observed in the study plot during the survey period. However, there were few established seedlings of *B. javanica* over the 19 yr. Although seeds of *B. javanica* can germinate even on a shaded forest floor under a dense canopy, whether or not germinated seedlings can establish depends on the amount of available light (Tanimoto and Toyoda 1996). Thus, the seedlings of *B. javanica* that germinated under a dense canopy are less likely to establish and grow. Closure of a canopy gap appears to prevent seedlings of *B. javanica* from establishing. Thus *B. javanica*, like *Pinus*, appears to be a shade-intolerant pioneer species.

Low mortality of *B. javanica* at small size, as compared with other native canopy tree species except for *S. mertensiana*, indicates that most individuals of *B. javanica* existing during the survey period probably established in an environment in which available light was adequate. Indeed, 88.4% of *B. javanica* individuals existing in the survey period established before 1987. This suggests that the first *B. javanica* need a canopy opening for establishment, and thereafter when advanced in growth they can survive under even a closed canopy. In a primary forest of the Bonin Islands, large saplings of *B. javanica* are able to survive under even a dense canopy (Shimizu 1988). Seedlings of *B. javanica* have physiological and morphological acclimation capacity in their leaves to high or low light conditions in comparison with several native dominant species found in early, mid-, and late-successional stages in the primary forest of the Bonin Islands (Yamashita et al. 2002). The high acclimation capacity of *B. javanica* may enable lower mortality of small trees as compared with some native species that dominate the forest even under a closed canopy.

Our results suggest that establishment of *B. javanica* depends on whether seeds of *B. javanica* can germinate and grow under a canopy gap before the canopy closure. Seedlings and saplings of *B. javanica* exhibit greater growth than native canopy tree species except for *S. mertensiana* under a canopy gap. Although there were few differences in growth between smaller trees of *B. javanica* and that of natives under a closed canopy, they show lower mortality than natives except for *S. mertensiana*. Regeneration and maintenance of the *B. javanica* population in the secondary forest depends on the frequency and intensity of disturbance. Forests in the Bonin Islands have been disturbed occasionally by typhoons or severe drought in the last 30 yr (Oka et al. 2000). Therefore, the forests in the Islands are likely to be subjected to disturbances in the future, which would allow the establishment and reproduction of *B. javanica* in the secondary forest.

Species richness of native tree species at the stand invaded by *B. javanica* in the *Pinus-Schima* forest after death of *P. luchuensis* was significantly lower than at sites where *B. javanica* had not invaded, which is likely to be due to strong negative correlations between distribution patterns of individuals of *B. javanica* and those of principal native tree species (K.H., unpubl. data). If the negative correlations are due to prevention of establishment of native species by *B. javanica*, then establishment and reproduction of *B. javanica* in the secondary forest may directly prevent the establishment of native tree species. However, increases in basal areas of many native species (Appendix 1) and frequent recruitment of several species such as *R. wrightiana* and *L. micranthum* (data not presented) oc-

curred even when *B. javanica* was present, and species richness of native species in our permanent study plot did not change during the survey period (Appendix 1 and 2). These results indicate that competition between *B. javanica* and native species during the survey period may have been weak because many vacant niches existed after the death of *P. luchuensis*. Our study period may have been too short to clarify effects of *B. javanica* on population dynamics of native species in the secondary forests. To clarify the effects, it is necessary to conduct a more long-term survey and also compare our results with the population dynamics of native species in the secondary forests that *B. javanica* did not invade.

Finally, it is interesting to note that an alien pine nematode that was introduced accidentally plays a key role as an unintended bicontrol agent for *P. luchuensis*. However, effects of *P. luchuensis* on native species in the secondary forest were minor because it appeared to occupy a vacant niche in the Bonin Islands, where there had been no native species with a growth form and physical features like pines (Shimizu and Tabata 1985). Nevertheless, the pine nematode may have substantial effects on native species in the secondary forest because basal area of native species in our study plot increased after death of *P. luchuensis*.

ACKNOWLEDGMENTS

We thank the Environmental Agency and the Department of National Forests in the Ogasawara Islands for permission to conduct this study on the plants of Chichijima Island. We are grateful to Masae Shiyomi, Yoshimichi Hori, Shinpei Sudo, Wakio Kimura, Satoru Honma, Takenao Takahashi, Atsushi Ishida, Takashi Nakano, Naoko Yamashita, and Keiichiro Yoshida for valuable discussion of the manuscript. Yoshikazu Shimizu kindly provided an unpublished manuscript and data about changes in light environments on the forest floor of *Pinus-Schima* secondary forests. Judy Noguchi edited the English of the manuscript. Three anonymous referees made numerous valuable comments that improved our original manuscript. This study was originally organized by the late Professor Emeritus Makoto Kimura and the late Masaki Funakoshi.

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Appendix 1

Basal Area (BA, $cm^2\ m^{-2}$) and Density (No., $400\ m^{-2}$) of Trees of All Woody Species in a 20 by 20 m Plot

Species	Family Name	1984 BA	No.	1987 BA	No.	1990 BA	No.	1995 BA	No.	1998 BA	No.	2000 BA	No.	2003 BA	No.
Alien species															
Bischofia javanica Blume	Euphorbiaceae	2.61	130	8.33	169	13.98	169	17.02	166	17.61	158	19.62	160	23.38	154
Caryota urens L.	Palmae					0.21	1	0.21	1	0.04	1	0.03	1	0.01	4
Cinnamomum camphora Presl	Lauraceae	1.79	2	1.89	2	2.16	4	2.43	4	2.60	4	2.65	4	2.74	4
Morus australis Poir.	Moraceae	<0.01	1	0.01	3	0.01	5	0.04	4	0.05	4	0.06	4	0.06	4
Mangifera indica L.	Anacardiaceae	3.38	1	3.43	1	3.67	1	3.86	1	4.02	1	4.14	1	4.78	1
Pinus luchuensis Mayer	Pinaceae	10.79	4	8.03	3	3.18	1	4.45	1						
Total of alien species		18.57	138	21.69	178	23.20	181	28.01	177	24.32	168	26.50	170	30.97	167
Native species															
Ardisia sieboldii Miquel	Myrsinaceae	0.07	6	0.16	11	0.24	19	0.26	20	0.27	20	0.17	22	0.31	27
Callicarpa subpubescens Hook. & Arn.	Verbenaceae			<0.01	1	<0.01	1	<0.01	1	<0.01	1	<0.01	1	<0.01	1
Cinnamomum pseudo-pedunculatum Hayata	Lauraceae			<0.01	2	0.01	4	0.02	7	0.05	7	0.06	8	0.07	10
Elaeagnus rotundata Nakai	Elaeagnaceae	0.05	1	0.01	1									<0.01	1
Elaeocarpus photiniifolius Hook. & Arn.	Elaeocarpaceae	<0.01	3	0.01	3	0.00	3	0.01	4	0.01	3	0.01	2		
Hibiscus glaber Masum.	Malvaceae	0.01	2	0.05	2	0.11	4	0.08	3	0.08	2	0.10	3	0.04	2
Ligustrum micranthum Zucc.	Oleaceae	0.02	5	0.03	13	0.08	49	0.12	47	0.12	32	0.13	30	0.11	24
Livistona chinensis R. Br. var. *boninensis* Becc.	Palmae	0.68	1	0.66	1	0.65	1	0.66	1	0.66	1	0.61	1	0.61	1
Machilus boninensis Koidz.	Lauraceae	<0.01	1	<0.01	1							0.04	1	0.04	1
Machilus kobu Maxim.	Lauraceae	0.03	8	0.16	20	0.22	21	0.27	17	0.31	14	0.29	14	0.31	14
Neolitsea aurata Koidz.	Lauraceae	0.03	3	0.06	9	0.11	12	0.13	14	0.15	12	0.12	10	0.12	9
Osmanthus insularis Koidz.	Oleaceae	0.01	5	0.36	11	0.16	16	0.31	17	0.44	17	0.49	18	0.55	20
Pandanus boninensis Warb.	Pandanaceae					2.00	10	2.27	11	2.26	11	2.45	12	1.35	7
Pittosporum boninense Koidz.	Pittosporaceae	0.04	2	0.09	4	0.14	4	0.18	4	0.17	2	0.18	2		
Pouteria obovata (R. Br.) H. L Lam	Sapotaceae	2.91	12	3.93	18	4.05	20	4.14	17	4.37	16	4.39	12	3.72	12
Rhaphiolepis wrightiana Maxim.	Rosaceae	2.65	80	2.71	91	3.10	120	2.50	101	3.26	87	3.10	80	3.05	63
Schima mertensiana (Sieb. & Zucc.) Koidz.	Theaceae	5.29	9	5.78	15	6.77	17	7.58	17	8.61	17	8.75	22	10.08	25
Syzygium cleyeraefolium (Yatabe) Makino	Myrtaceae													0.00	1
Tarenna subsessilis (A. Gray) Ohwi	Rubiaceae	0.01	1	0.01	1	0.01	1	0.01	1	0.01	1	0.01	1		
Wikstroemia pseudoretusa Koidz.	Thymelaeaceae													<0.01	1
Total of native species		11.64	139	13.77	204	17.20	302	18.03	282	20.22	243	20.43	239	19.81	219
Total of tree species		30.21	277	35.46	382	40.41	483	46.05	459	44.54	411	46.93	409	50.78	386

Appendix 2

Density (400 cm^{-2}) of Saplings of All Woody Species in a 20 by 20 m Plot

Species	Family Name	1984	1987	1990	1995	1998	2000	2003
Alien species								
Bischofia javanica Blume	Euphorbiaceae	68	61	32	22	21	18	12
Caryota urens L.	Palmae	1				1	1	1
Morus australis Poir.	Moraceae	5	3	1	1	1	4	1
Psidium cattleianum Sabine	Myrtaceae					2	3	2
Psidium guajava L.	Myrtaceae						1	
Total of alien species		74	64	33	23	25	27	16
Native species								
Ardisia sieboldii Miquel	Myrsinaceae	28	20	23	20	21	25	25
Callicarpa subpubescens Hook. & Arn.	Verbenaceae	1						1
Celtis boninensis Koidz.	Ulmaceae							1
Cinnamomum pseudo-pedunculatum Hayata	Lauraceae	15	13	10	11	7	13	7
Elaeagnus rotundata Nakai	Elaeagnaceae						1	2
Elaeocarpus photiniifolius Hook. & Arn.	Elaeocarpaceae	5	2	2	1	2		
Euonymus boninensis Koidz.	Celestraceae	3	2	3				
Hibiscus glaber Masum.	Malvaceae					1	9	7
Ligustrum micranthum Zucc.	Oleaceae	216	143	93	58	46	62	24
Machilus boninensis Koidz.	Lauraceae	2	1	1	1	1		
Machilus kobu Maxim.	Lauraceae	20	16	11	9	12	17	17
Neolitsea aurata Koidz.	Lauraceae	14	10	11	7	7	9	15
Osmanthus insularis Koidz.	Oleaceae	17	10	6	7	7	11	17
Pandanus boninensis Warb.	Pandanaceae	27	2	15	10	10	7	2
Pittosporum boninense Koidz.	Pittosporaceae	2	1	2	1	1	1	1
Pouteria obovata (R. Br.) H. L Lam	Sapotaceae	141	106	100	69	60	60	61
Rhaphiolepis wrightiana Maxim.	Rosaceae	251	220	197	152	215	288	195
Schima mertensiana (Sieb. & Zucc.) Koidz.	Theaceae	11	10	10	9	10	14	14
Syzygium cleyeraefolium (Yatabe) Makino	Myrtaceae	2	2	1	1			1
Tarenna subsessilis (A. Gray) Ohwi	Rubiaceae	3	3	2	1	1		
Trema orientalis Blume	Ulmaceae	3						
Wikstroemia pseudoretusa Koidz.	Thymelaeaceae				3	6	3	
Total of native species		761	561	487	360	407	520	390
Total of tree species		835	625	520	383	432	547	406

Appendix 3

Species Composition of *Pinus-Schima* Secondary Forests after Death of *P. luchuensis* on Chichijima Island

Species	No. of Trees (No. 0.487 ha^{-1})	Density (No. ha^{-1})	Basal Area (ha^{-1})	Max. DBH (cm)	Frequency of Occurrence (No. 35 plots^{-1})
Alien species					
***Bischofia javanica* Blume**	495	1,016.43	6.37	**63.7**	17
Caryota urens L.	12	24.64	0.09	12.0	3
Casuarina equisetifolia Forst.	1	2.05	0.02	11.5	1
Chrysalidocarpus lutescens H. Wendl.	1	2.05	<0.01	4.2	1
Cinnamomum camphora (L.) J. Presl	6	12.32	0.27	27.4	3
Diospyros ferrea (Willd.) Bakh.	10	20.53	<0.01	6.1	3
Leucaena leucocephala (L.) de Wit	2	4.11	<0.01	4.1	2
Mangifera indica L.	1	2.05	0.39	49.4	1
Morus australis Poir.	7	14.37	0.06	12.9	3
Pinus luchuensis Mayer	40	82.14	2.17	59.1	9
Psidium cattleianum Sabine	208	427.10	0.14	6.1	24
Native species					
Ardisia sieboldii Miquel	395	811.09	0.52	13.2	23
Boninia glabra Planchon	2	4.11	<0.01	2.8	1
Callicarpa subpubescens Hook. Et Arn.	9	18.48	0.01	5.2	7
Cinnamomum japonicum Sieb. ex Nakai	1	2.05	<0.01	0.4	1
Cinnamomum pseudo-pedunculatum Hayata	64	131.42	0.11	11.0	18
Cyathea mertensiana (Kunze) Copel.	3	6.16	0.13	16.8	2
Distylium lepidotum Nakai	10	20.53	0.01	4.6	3
Drypetes integerrima (Koidz.) Hurusawa	2	4.11	<0.01	5.0	2
Elaegnus rotundata Nakai	1	2.05	<0.01	0.9	1
***Elaeocarpus photiniifolius* Hook. et Arn.**	45	92.40	1.26	**38.1**	10
Fagara boninsimae Koidz.	17	34.91	0.08	12.7	8
Ficus boninsimae koidz.	1	2.05	<0.01	0.5	1
Ficus nishimurae koidz.	1	2.05	<0.01	2.0	1
Freycinetia boninensis Nakai	11	22.59	0.01	3.3	2
Geniostoma glabrum Matsum.	1	2.05	0.02	11.5	1
Hernandia ovigera L.	1	2.05	<0.01	0.4	1
Hibiscus glaber Masum.	81	166.32	1.10	17.7	9
Ilex mertensii Maxim.	13	26.69	0.04	9.2	10
Ligustrum micranthum Zucc.	179	367.56	0.10	6.2	24
Livistona chinensis R. Br. Var. Boninensis Becc.	29	59.55	2.09	28.8	9
Mahcilus boninensis Koidz.	1	2.05	<0.01	4.7	1
***Machilus kobu* Maxim.**	287	589.32	1.52	**25.5**	29
Neolitsea aurata Koidz.	176	361.40	0.74	19.6	15
Ochrosia nakaiana Koidz.	10	20.53	0.05	9.0	4
Osmanthus insularis Koidz.	95	195.07	0.25	13.9	22
Pandanus boninensis Warb.	28	57.49	0.46	13.8	10
Photinia wrightiana Maxim.	8	16.43	0.01	2.2	3
Pisonia umbellifera Seem.	1	2.05	<0.01	0.9	1
***Pouteria obovata* (R. Br.) H. L Lam**	94	193.02	1.08	**30.4**	20
Rhaphiolepis wrightiana Maxim.	436	895.28	1.48	23.0	29
Rhus succedanea L.	8	16.43	0.02	7.6	3
***Schima mertansiana* (Sieb. et Zucc.) Koidz.**	1,341	2,753.59	30.84	**78.0**	35
Syzygium cleyeraefolium (Yatabe) Makino	61	125.26	0.14	10.6	14
Tarenna subsessilis (A. Gray) Ohwi	2	4.11	<0.01	1.7	2
Trema orientalis Blume	16	32.85	0.02	5.5	2
Wikstroemia pseudoretusa Koidz.	8	16.43	<0.01	1.3	3
Total of tree species	4,221	8,667.35	51.62		394